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Bisbalia vossi n. g., n. sp. (Nematoda: Onchocercidae), a filarial worm from a geomyoid rodent, *Heteromys anomalus*, in Venezuela

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Abstract

Bisbalia vossi n. g., n. sp. is described from *Heteromys anomalus* (Rodentia: Geomyoidea: Heteromyidae) in northern Venezuela (Aragua). The filariae were found in a membranous pocket in the pleural cavity, and almost all had ingested red blood cells of their host. The morphology of this onchocercine species is highly evolved (advanced reduction of head and caudal papillae; short undivided oesophagus). Its very short microfilariae (60 μm) and the shape of the tail of the female (two terminal median pairs of bosses) suggest that this species could be derived from *Ackertia* Vaz, 1934, a South American genus parasitic in caviomorph rodents which is related to the *Dipetalonema*-line, but *Ackertia* has several pairs of precloacal papillae, which are absent in the new genus. In North America, where the geomyoid rodents originated and diversified, the two previously described filarial species differ from this new material and show affinities with Old World bat parasites (*Litomosa* van Beneden, 1871).

Introduction

Only two North American congeneric species of filariae have been described from the rodent superfamily Geomyoidea (see Gardner & Schmidt, 1986). Initially placed in *Litomosoides* Chandler, 1931, species of which are parasitic in terrestrial and flying New World mammals, they were recently shown to have more affinities with *Litomosa* van Beneden, 1872 from Old World bats (Guerrero et al., 2002). The hosts of these filariae belong to the family Geomyidae, which is restricted to North America. New material was recovered from a heteromyid rodent in South America. It appeared to have no resemblance to the two North American filarial species and to represent a new onchocercid genus.

Materials and methods

Two spiny pocket mice *Heteromys anomalus* (Thompson) deposited in the collections of mammals in the Museo de Biologia, Instituto de Zoologia Tropical, Facultad de Ciencias, Universidad Central de Venezuela, were kindly made available for dissection, and one harboured filariae (no. MBUCV I-02775). Both rodents had been trapped in November, 1979, near a narrow stream at the Estacion Biologica de Rancho Grande, Parque National Henri Pittier, at 900–1,000 m altitude in the Cordillera de la Costa, NW Maracay, Estado Aragua, Venezuela; it is an area of lowland rain forest (Voss, 1988).

The worms lay in the thoracic cavity, between the lungs and the heart and close to the dorsal wall; they were coiled in a membranous pocket and a clot of red blood cells surrounded the posterior region of one male which was closely enveloped by the membrane. Heart blood of the infected rodent was teased out and examined for microfilariae but none were found.

Worms were cleared in lactophenol. Apical and transverse sections of the body were made with a razor-blade. The morphology of the head in apical, lateral and median view was studied in several male

and female specimens. Spicules were dissected out to study their detailed morphology. Fully-developed microfilariae were removed from the ovijector for study. The length of adults is given in millimetres; all other measurements are in micrometres.

Bisbalia n. g.

Diagnosis
Onchocercinae with short oesophagus (≤ 400 μm) without distinct glandular part; very small buccal capsule reduced to tiny ring; reduced number of head papillae; no caudal lappets. Male with 2–3 pairs of paracloacal papillae often grouped on nipple; *area rugosa* with transverse bands of longitudinal crests; left spicule with membranous blade; right spicule with 2 sclerified lateral walls extend to round extremities. Female opisthodelphic; 3–4 flattened muscle cells per quadrant; vagina bent, with sphincter; tail with two median pairs of terminal bosses. Small microfilariae (60 μm long) without sheath, with very tiny cephalic hook and nucleated caudal point. Type-species *B. vossi* n. sp.

Bisbalia vossi n. sp.

Type-host: *Heteromys anomalus* (Thompson), Heteromyidae, Geomyoidea.
Site of infection: Pleural cavity, in a membranous pocket.
Type-locality: Rancho Grande, Parque National Henri Pittier, Maracay, Venezuela.
Type-material: Male holotype and 4 male paratypes; female allotype and 4 female paratypes, 2 long posterior fragments of female paratypes. The holotype and allotype are deposited in the Museo de Biologia de la Universidad Central de Venezuela (MBUCV), no. I-02775; paratypes are deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN), no. 89 CV.
Etymology: The genus is named for our Venzuelan colleague, Dr Francisco Bisbal, Director of the Estacion Biologica Rancho Grande. The species is named for the mammalogist Dr R. Voss who captured and identified the rodent host species.

Description (Figures 1, 2; Table 1)

Measurements of adults are given Table 1 and their morphology is illustrated in Figures 1 and 2. Head with 2 very small papillae, 1 dorsal, 1 ventral; 2 amphids with oblique conspicuous channels. Small mouth; tiny buccal cavity; buccal capsule a very small ring, its height hardly greater than head cuticle in thickness; in apical view, lumen of the cavity round anteriorly, irregularly incised posteriorly. Short oesophagus with Y-shaped lumen; no distinct glandular part; oesophageal nuclei apparently small in number and constant in position. Intestine wide anteriorly. Red blood cells were identified in oesophageal and intestinal lumens of several specimens. Body cuticle with internal lateral thickenings, more pronounced in anterior region. Musculature formed from small number of cells, *c.* 3–4 per quadrant at mid-body.

Male. Thick musculature; lateral chord with 2 columns of nuclei. Caudal papillae not numerous and grouped near cloacal aperture; 2–3 pairs present, often fused and forming nipple laterally on each side. Rounded caudal extremity, smooth or with very tiny terminal point or group of 3 points. *Area rugosa* beginning anterior to cloacal aperture and extending to coiled posterior part of body; composed of transverse bands of irregular longitudinal crests. Left spicule with distinct handle and blade; blade with 2 lateral alae, folded longitudinally, its distal end with 3 filamentous points; ellipsoidal gametes were identified on blade of 1 male. Right spicule without dorsal heel, curtailed at its distal extremity; ventral wall of right spicule well sclerified in anterior mid-part only; 2 sclerified lateral-dorsal walls end distally in 2 thick lateral rounded extremities which guide left spicule; these extremities with membranous fringe.

Female. Posterior third of body regularly attenuated. Musculature thick anteriorly, thin at mid-body; lateral chords with 4 columns of nuclei. Vulva posterior to oesophago-intestinal junction; vagina subspherical, well developed, with 2 bends and posterior cellular sphincter; ovijector widens prior to dividing into 2 uteri. Uteri straight and parallel. Oviducts long. Opisthodelphic; rounded apex of ovaries more or less far from tail depending to state of maturation of filaria. Tail long, only slightly bent ventrally, often with oblique extremity; 2 pairs of subterminal bosses, 1 ventral, 1 dorsal. Four females had uterine microfilariae in variable numbers. Most of females were fertilised and, in some of them, round spermatozoa were still present in anterior part of uteri, indicating recent mating.

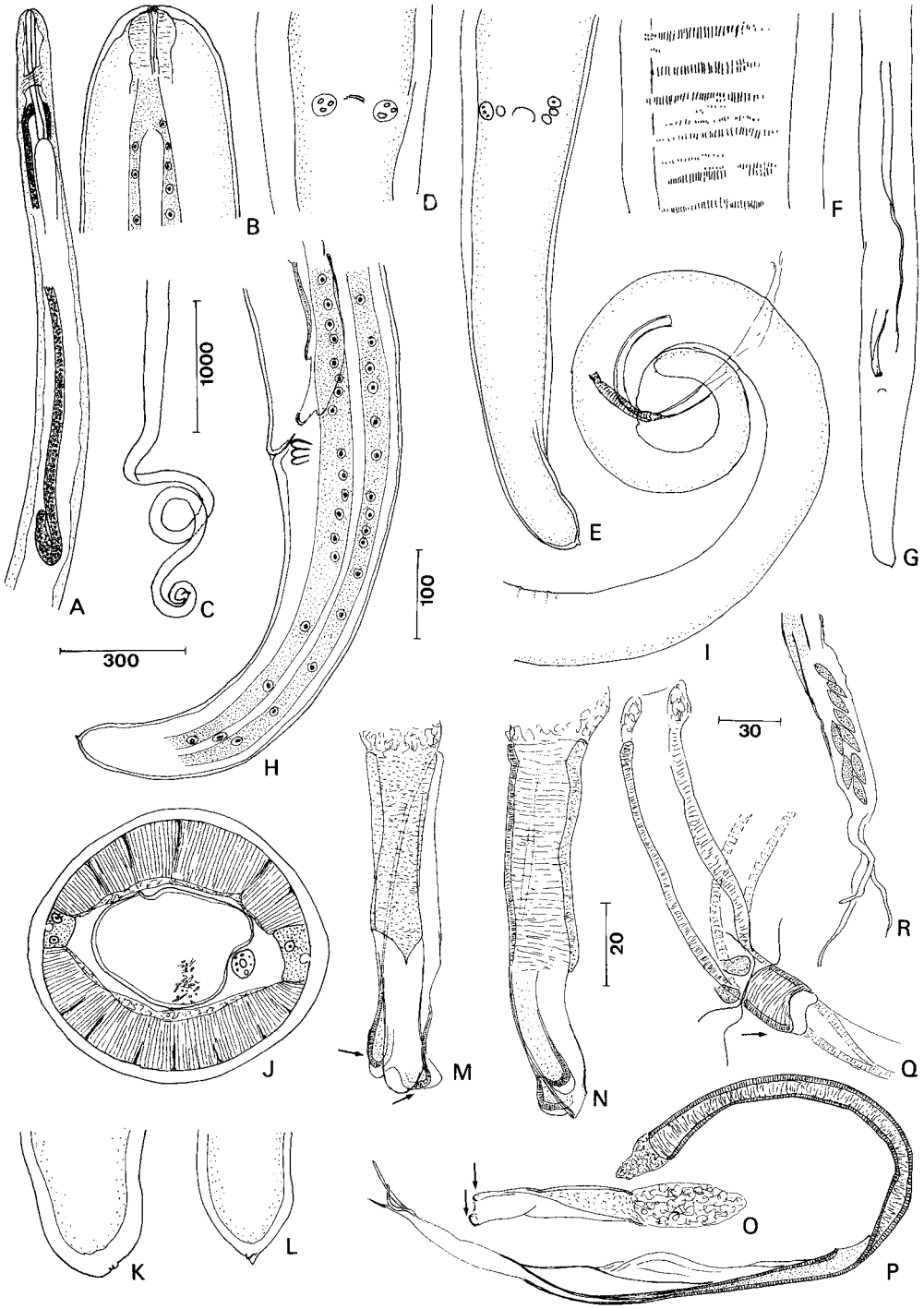

Figure 1. Bisbalia vossi n. g., n. sp. Males. A. Anterior region, left lateral view. B. Cephalic region, lateral view (the beginning of the lateral chord is shown). C. Posterior coiled region. D. Papillae close to the cloacal aperture, ventral view. E. Another specimen, tail, ventral view. F. Detail of *area rugosa*, ventral view. G. Posterior region, ventral view. I. Another specimen, caudal region, lateral view. J. Transverse section of body at mid-length. K. Distal extremity of a male, right lateral view. L. *Idem*, another specimen. M. Right spicule, ventral view, after dissection. N. *Idem*, right lateral view (the sclerified lateral rounded extremities are indicated by arrows). O. Right spicule, ventral view (from the male shown in Figure 2G.). P. Left spicule. Q. Detail of the cloacal region, with two pairs of papillae on a nipple and the right spicule guiding the left one. R. Distal extremity of the blade of the left spicule, with male gametes. *Scale-bars*: A, 300 μm; B,D,E,F,H,J,O,Q, 30 μm; C, 1000 μm; G, I, 100 μm; K,L,M,N,P,R, 20 μm.

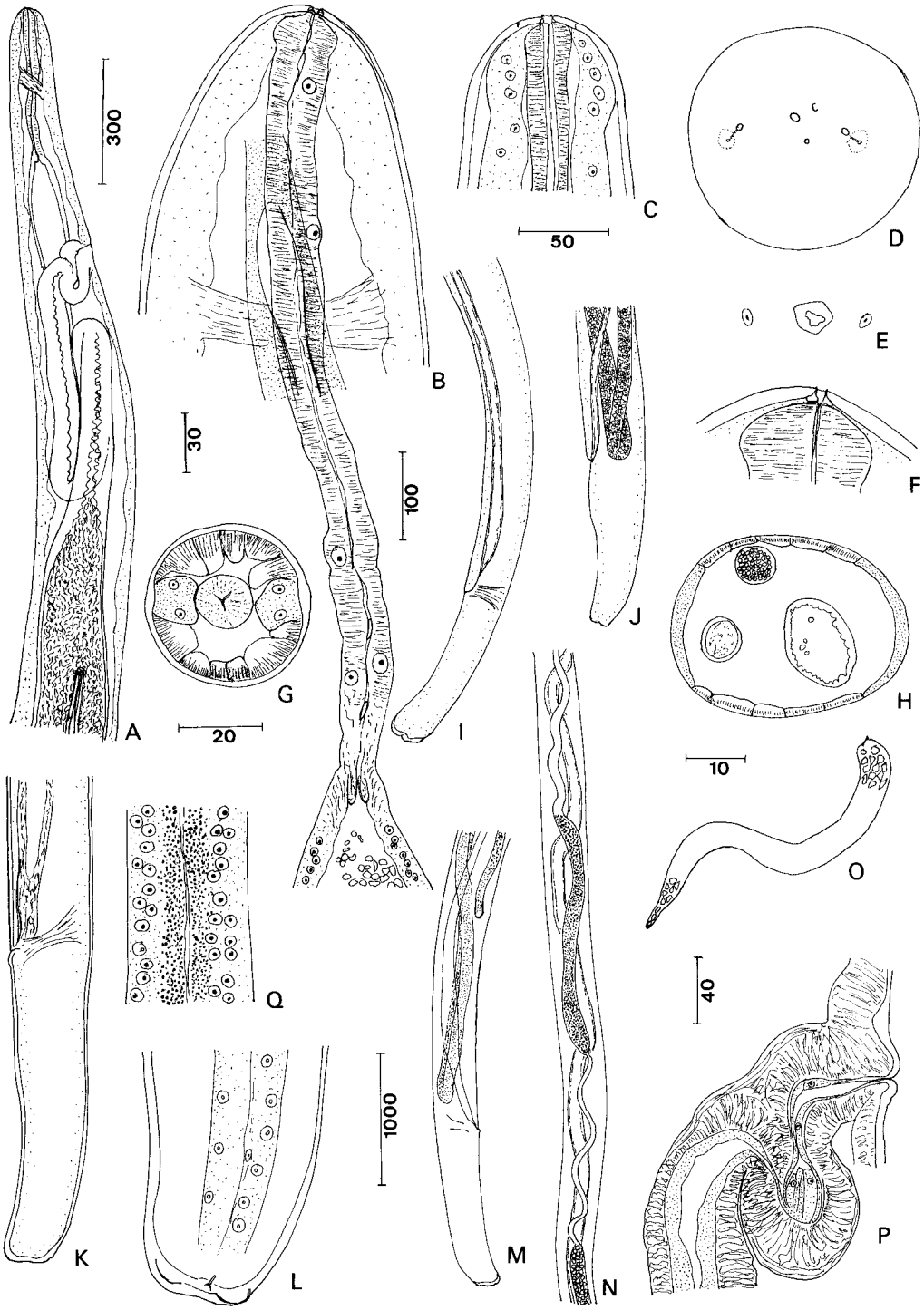

Figure 2. Bisbalia vossi n. g., n. sp. Females. A. Anterior region, left lateral view. B. Head and oesophagus (the beginning of the lateral chord is shown). C. Head, median view. D. Head, *en face* view. E. Base of the buccal capsule, transverse optical section, at level of amphidial channels. F. Region of the buccal capsule. G. Transverse section of the body at the level of the oesophagus. H. *Idem*, at mid-body. I. Caudal region, right lateral view. J. *Idem*, another female. K. Tail, another specimen. L. Caudal extremity, right lateral view, from another specimen. M. Same specimen, posterior region. N. Oviducts and beginning of uteri (filled with male gametes). O. Microfilaria, dissected out from the ovijector. P. Vagina, left lateral view. Q. Lateral chord at level of oesophago-intestinal junction. *Scale-bars*: A,I,J,M, 300 μm; B,G, 30 μm; C, 50 μm; D,E,F,L,Q, 20 μm; H,K, 100 μm; N, 1,000 μm; O, 10 μm; P, 40 μm.

Table 1. Bisbalia vossi n. g., n. sp.

Males		Holotype	M 1	M 2	M 3	M 5	Mean
Length (mm)		24.7	24.0	25. 7	26.6	27.8	25.8
Width:	maximum	189	172	172	180	192	181
	at nerve-ring	70	83	100	88	69	82
	at end of oesophagus	88	91	115	107	78	96
Buccal capsule		4.0 × 8.0	4.0 × 8.0	4.0 × 8.0	4.6 × 8.0	3.3 × 7.0	4.0 × 7.8
Oesophagus		372 × 20	329 × 23	294 × 24	356 × 23	314 × 22	333 × 22
Nerve-ring		166	180	163	182	166	171
Tail		330 × 65	309 × 71	341 × 84	329 × 81	307 × 67	323 × 74
Left spicule (handle)		320 (138)	336 (163)	319 (136)	300 (143)	332 (149)	319 (146)
Right spicule		97	94	92	98	96	95
Spicule-ratio		3.3	3.47	3.47	3.06	3.46	3.35
Area rugosa:	from cloaca	740 - 3,368	1,128 - 3,163	714 - 2,851	748 - 2,468	700 - 3,000	806 – 2,970
	crest height	2-5	1-6	2-6	2-7	2-4	3.9
	band distance	10-20	12-15	7-14.0	12-23	11	13.7
Females		Allotype	F 1	F 2	F 3	F 5	Mean
Length (mm)		49.9	50.1	59.9	46.6	-	51.6
Width:	maximum	321	331	365	297	-	328
	at nerve-ring	130	113	106	130	141	124
	at end of oesophagus	161	147	159	172	180	164
	at vulva	175	192	214	197	209	197
Buccal capsule		3.5 × 5.8	3.8 × 7.0	2.4 × 8.0	4.6 × 7.8	-	3.6 × 7.2
Oesophagus		350 × 25	390 × 31	358 × 29	376 × 28	389 × 25	370 × 28
Nerve-ring		149	155	121	158	158	165
Vulva		462	609	740	598	530	586
Vagina		152 × 90	146 × 90	152 × 85	175 × 82	152 × 85	155 × 86
Ovijector length		1,210	1,025	1,260	1,410	?	1,226
Tail		490 × 104	377 × 101	570 × 152	507 × 138	-	486 × 123

Microfilaria: Small; no sheath identified; body wider in anterior third; head with very tiny cephalic hook; short cephalic space. Posterior region ends in short point containing 3 elongate, aligned nuclei; no anucleate terminal region. Measurements (microfilariae extracted from ovijector of 1 female): 63, 60, 65, 72, 65 long, 5-5.5 wide.

Differential diagnosis

This filaria has such a reduced buccal ring that it is clearly distinct from the two known species from the Geomyidae, *Litomosa westi* (Gardner & Schmidt, 1986 and *Litomosa thomomydis* (Gardner & Schmidt, 1986). It is also different from the other species of *Litomosa* and those of the closely related genus *Litomosoides*, both of which are characterised by a robust and complex buccal capsule, its posterior part being within the apex of oesophagus. The microfilariae are also distinct from those of these two genera (Guerrero et al., 2002): they do not have the posterior third of the body reflexed within a shorter sheath, as in *Litomosa*, and they are not attenuated anteriorly and terminated by a salient cephalic hook, as in *Litomosoides*.

The specimens from *H. anomalus* are highly evolved, making their relationships more difficult to establish. The tail being longer than wide and lacking caudal alae are characters of the Onchocercinae Leiper, 1911 and Splendidofilariinae Chabaud & Choquet, 1953.

Splendidofilariines have a reduced buccal cavity, short undivided oeosphagus and a small number of caudal papillae near the cloacal aperture, like our specimens, but in general they have subequal spicules (Anderson & Bain, 1976). However, one genus, *Paronchocerca* Peters, 1936, a parasite of birds, has unequal

and dissimilar spicules and a complex vagina, as in our specimens. In addition, several of its species have an *area rugosa* of similar shape and the right spicule ends with two bows. However, important characters distinguish *Paronchocerca* from our specimens: the eight voluminous symmetrically arranged head papillae, the caudal papillae arranged in a postanal half circle and the shorter tail (ratio 2-2.5 instead of 4).

The filaria from *H. anomalus* is better placed in the Onchocercinae. Among the taxa listed in the key of Anderson & Bain (1976), two South American genera show some resemblances in their female caudal extremity: *Ackertia* Vaz, 1934, from caviomorph rodents, and *Migonella* Lent, Freitas & Proença, 1946, from a bat. *Ackertia* also has small microfilariae (60 μm long) and a reduced buccal cavity, but a less atrophied buccal capsule and differently arranged caudal papillae (two rows of precloacal papillae; Bain & Hocquet, 1968). *Migonella* differs in its extremely small size and apparently more reduced buccal capsule and sensory organs (Lent et al., 1946).

The following genera or subgenera of Onchocercinae described after the publication of the CIH keys (filarial section) are also distinct from our specimens:
Cruorifilaria Eberhard, Morales & Orihel, 1976, a parasite of the caviomorph rodent *Hydrochoerus hydrochaeris* (L.) (capybara) in Colombia, is particularly distant: it is a robust worm, with a spirally coiled body, larger mouth and buccal cavity, longer oesophagus (*c.* 2 mm), eight well-developed head papillae, and more numerous and differently arranged caudal papillae (Eberhard et al., 1976).
Chabfilaria Bain, Purnomo & Dedet, 1983, a parasite of sloths (*Choloepus didactylus* (L.), Edentata, suborder Xenarthra) presents affinities with the Setariinae, which were absent from our specimens (Bain et al., 1983).
Yatesia Bain, Baker & Chabaud, 1982 (= *Alifilaria* Yates & Jorgeson, 1983), from *H. hydrochaeris* in Colombia, has a small mouth and small ring, but the oesophagus is divided and very long (4 mm), lateral alae are present along the body, precloacal papillae are numerous and the microfilaria is large with a long anucleate posterior region (Yates, 1982; Yates & Jorgeson, 1983).
Dasypafilaria (Eberhard, 1982) Chabaud & Bain, 1994, parasites of the Xenarthra, is very small (3.8–9.5 mm) and has a well developed and strongly cuticularised buccal capsule, a divided and relatively long oesophagus, eight head papillae, caudal lappets, a few pairs of caudal papillae far behind the cloacal aperture and large microfilariae, 284-394 /7–9 μm (Eberhard, 1982).
Cherylia Bain, Petit, Jacquet-Viallet & Houin, 1985, a parasite of the Didelphidae, has a more primitive morphology as shown by the divided oesophagus and well-developed sensory organs (Bain et al., 1985).
Cercopithifilaria Eberhard, 1980 (raised to full generic rank by Bain, Baker & Chabaud, 1982), which is world-wide and has a large mammalian host range (Uni et al., 2001), is an evolved genus with a reduced buccal capsule and an undivided oesophagus as in our specimens, but it differs in the presence of caudal lappets, the arrangement of the caudal papillae, the shape of the vagina and spicules, the flattened oesophageal lumen and the larger microfilariae.
Strianema Eberhard, Orihel & Campo-Aasen, 1993, a parasite of *Dasypus* spp., has caudal lateral alae, 12 pairs of caudal papillae and no buccal ring (Eberhard et al., 1993). Because of these characters, the validity of *Strianema*, previously synonymised with *Cercopithifilaria* by Chabaud & Bain (1994), has recently been confirmed (Bain et al., 2002).

Conclusions

The great generic diversity of the Onchocercinae in South America has already been emphasised (Bain et al., 1982). These genera, often monospecific, are parasites of endemic Neotropical mammals, Didelphidae, Xenarthra and caviomorph rodents. This is not the case with *Bisbalia* n. g.

The Geomyoidea originated in North America in mid-Eocene (Hartenberger, 1998) and diversified in this region. Some heteromyids migrated recently into South America, when this continent was joined to North America, during the Pleistocene (3 mya). Several species are known in Central America, whereas only two species of *Heteromys, H. anomalus* and *H. australis* Thomas, are present in South America, restricted to the nothern part of this continent, from Ecuador to Venezuela (Anderson et al., 2002). Either *H. anomalus* arrived with its parasite and *Bisbalia* is a North American filarial genus for which representatives remain to be discovered in this region, or *H. anomalus* acquired its filaria from the South American parasitic fauna. It could then be a form derived from *Ackertia* parasitic in caviid rodents. Indeed, the two genera have a similar female caudal extremity with median bosses and a very short microfilaria.

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